

EGG AND LARVAL DRIFT OF THE ANTARCTIC FISH *NOTOTHENIA CORIICEPS*

by

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ABSTRACT. - The drift of eggs and larvae of the Antarctic fish *Notothenia coriiceps* is described from material collected between 1975 and 1988. Spawning is probably demersal. The fertilized eggs ascend to surface waters and are pelagic until hatching. They drift into oceanic waters where they hatch in late November/early December (Antarctic Peninsula). The larvae are neustonic and drift with the Antarctic Circumpolar Current. They are dispersed across the Scotia Sea and may drift as far as South Georgia, providing evidence of gene flow to other fish populations. The pelagic 'blue phase' juveniles may spend the winter and second summer in the midwaters before transition to the demersal phase, although this transition may occur by the end of the first summer. The complete lack of larvae during summer and fall suggested that the egg and larval population is dispersed from Bransfield Strait and adjacent waters. Recruitment to this area is likely to be provided from the south-west with the Circumpolar Current. The life cycle of *N. coriiceps* is compared with other nototheniid fishes showing similar early life history characters. The adaptive significance for Antarctic fishes to produce large pelagic eggs is discussed.

RÉSUMÉ. - La dispersion des oeufs et des larves de *Notothenia coriiceps* est décrite à partir de matériel collecté entre 1975 et 1988. La ponte est probablement démersale. Les oeufs fécondés remontent vers les eaux de surface et sont pélagiques jusqu'à l'éclosion. Ils se dispersent dans les eaux océaniques où ils éclosent fin novembre/début décembre (Péninsule Antarctique). Les larves sont neustoniques et dérivent avec le courant antarctique circumpolaire. Elles sont dispersées dans toute la mer d'Ecosse et peuvent dériver jusqu'en Sud Géorgie, ce qui met en évidence l'apport génétique vers d'autres populations de cette espèce. Les juvéniles pélagiques en "phase bleue" peuvent passer l'hiver et le second été dans les eaux intermédiaires avant leur transition vers la phase démersale, bien que cette transition puisse se passer à la fin du premier été. L'absence totale de larves pendant l'été et l'automne suggère que les oeufs et les larves sont dispersées à partir du détroit de Bransfield et des eaux voisines. Le recrutement vers cette zone provient probablement du sud-ouest avec le courant circumpolaire. Le cycle vital de *N. coriiceps* est comparé à celui de poissons nototheniides possédant de semblables stades de développement. La signification de l'adaptation des poissons de l'Antarctique à produire des oeufs pélagiques de grande taille est discutée.

Key-words. - Nototheniidae, *Notothenia coriiceps*, Antarctic, Eggs, Larvae, Drift.

The Antarctic nototheniid *Notothenia coriiceps* Richardson (= *Notothenia coriiceps neglecta* Nybelin) has a wide circumantarctic distribution and is an abundant fish in nearshore waters down to depths of 450 meters (DeWitt, 1977; Kock, 1989). Its nearshore availability and abundance has led to numerous studies dealing with the various aspects of its biology, such as reproduction (e.g., Everson, 1969; Kock, 1989), early life history (Norman, 1938; White *et al.*, 1982), food (e.g., Richardson, 1975), physiology (e.g., Johnston and Camm, 1987; Dunn *et al.*,

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1989), embryogenesis and genetics (Twelves and Bachop, 1980; Phan *et al.*, 1987), and population dynamics (Hureau, 1970; Everson, 1970). The life cycle was thought to be similar to that of the closely related *N. rossii* (White *et al.*, 1982). Spawning of *N. coriiceps* occurs in May/June (Kock and Kellermann, 1991), and the fishes migrate into deeper water before spawning (Everson, 1970; Hureau, 1970; Kock, 1989). Larvae hatch in October at South Georgia (White *et al.*, 1982). The pelagic 'blue phase' juveniles seem well adapted to a prolonged epipelagic existence, and significant morphological and physiological changes occur at the transition to the demersal phase (Norman, 1938; Johnston and Camm, 1987).

Large pelagic eggs with obviously nototheniid embryos were collected during the (West) German Antarctic expeditions to the Scotia Sea and the Antarctic Peninsula since 1975. These eggs were thought to belong to a *Notothenia* species, but could not be properly identified due to the lack of distinguishing characters. With the description of early larvae of *N. rossii* from the Kerguelen Islands by Camus and Duhamel (1985), however, it became possible to identify the eggs as those of *N. coriiceps* (North and Kellermann, 1990; Kellermann, 1990). Further, recently spawned eggs of the species collected in the field in early winter were identified by comparison of their surface structures with those of oocytes stripped from ripe females (Riehl and Kock, 1989).

Most nototheniid fishes probably have demersal eggs and nest guarding is known from several genera (Kock and Kellermann, 1991). In addition to *Notothenia coriiceps*, pelagic eggs were reported for other fishes of the genus, *Notothenia microlepidota* off New Zealand (Robertson, 1975), and probably also *N. rossii* at the Kerguelen Islands (Camus and Duhamel, 1985), and for *Dissostichus eleginoides* (Kellermann, 1990). An extensive off-shore dispersal of fingerling stages was observed off South Georgia (White *et al.*, 1982). Taking into account the long incubation period of several months, pelagic eggs of polar fishes may drift over long distances. Oceanic records of young *Notothenia* in epipelagic waters at great distances from islands and continents have been reported (Andriashev, 1965).

This paper reports on the distribution of eggs, larvae and juveniles of *N. coriiceps* caught in Antarctic Peninsula waters and in the Scotia Sea between 1975 and 1988. It examines the variations of egg size and of the egg and larval distribution. Larval growth in the field is derived from length data obtained during one summer season. Gene flow by advection to other populations by egg and larval drift and a circumantarctic recruitment pattern of *N. coriiceps* is suggested.

MATERIAL AND METHODS

Eggs, larvae and juveniles of *Notothenia coriiceps* were collected during six German expeditions to South Georgia, the Scotia Sea and to the Antarctic Peninsula between 1975 and 1988. In the 1975-76 season, primarily krill oriented surveys were carried out in the Scotia Sea, around South Georgia (November-April), and in Bransfield Strait and adjacent waters (Sahrhage *et al.*, 1978). In 1977-78, these areas were again surveyed with emphasis on South Georgia and the Antarctic Peninsula (Hempel *et al.*, 1979). During the spring of 1983, 1984 and 1987, standardized station grids were sampled in Bransfield Strait and adjacent waters (Fütterer, 1984; Hempel, 1985; Sahrhage, 1989). The marginal pack-ice zone in the north-western Weddell Sea between Elephant Island and the South Orkney Islands was investigated in 1988 (EPOS I, Hempel, 1989).

Eggs, larvae and juvenile fishes were caught using an opening-closing rectangular midwater trawl (RMT 1+8), or its multiple version, the RMT 1+8M (Baker *et al.*, 1973; Roe and Shale, 1979), and by a neuston catamaran (David, 1965). The fishing ranges of the RMT were within the upper 300 meters of the water column. The neuston-net fished in the top 20 cm of the surface layer with

two nets fishing at 20-10 cm and 10-0 cm. Mesh sizes were 350 and 4500 μm in the RMT 1 and RMT 8, respectively, and 300 μm in the neuston nets.

In 1975-76, four N-S-transects with 35 RMT and Neuston-net stations were worked in the Drake Passage and in the western part of the Scotia Sea (55°30' W - 40°00' W) from November 28-December 8, 1975 (Fig. 3). Another SW-NE-transect with 9 RMT and Neuston-net stations was worked December 22-27, 1975. The same area was sampled again on two transects with 13 RMT and Neuston-net stations from February 24-30, 1976 (Fig. 3). The central and eastern parts of the Scotia Sea were sampled on four transects with a total of 35 stations from March 23-April 4, 1976 (Fig. 3). In 1977-78, two SW-NE-transects across the central Scotia Sea with a total of 19 RMT and neuston-net stations were made November 12-16 and December 7-14, respectively (Fig. 4). Further 20 stations in the southwestern and northeastern parts of the area were worked January 21-28, and January 31-February 1, and another 10 stations March 5-7 and March 28-29, 1978 (Fig. 4). Sampling effort in 1977-78 focused chiefly on the Antarctic Peninsula area and on the north-eastern shelf of South Georgia; during the three legs of the expedition grids of RMT and neuston stations were fished there repeatedly between November and April (Hempel *et al.*, 1979).

In the austral spring of 1983, 1984 and 1987, similar grids of RMT stations were worked along the Peninsula (Fig. 1a-d); only part of the grid was sampled in 1984 due to technical problems, whereas the study area in 1987 extended down to 67° S (Sahrhage, 1986, 1989). During the 1988 cruise (EPOS I; Hempel, 1989), four N-S-transects were worked with the RMT and, where possible, with the neuston-net along the marginal pack-ice zone in the northeastern Weddell Sea, October 18-November 15, 1988.

Eggs, larvae and juvenile fishes were sorted from the total, unsplit plankton samples in the lab or during the cruise on board the ship. Fish were preserved in 4% buffered seawater - formaldehyde. During the 1988 cruise, eggs of *N. coriiceps* were used for age validation experiments and reared in tanks in a controlled temperature container laboratory (Kellermann, 1989b). Eggs, larvae and juveniles were measured under a dissection microscope to the nearest 0.1 mm. All lengths refer to standard length (SL), used synonymously with larval notochord length. SL can be converted to total length (TL) by using the equation $TL = -3.0124 + 1.2888 \cdot SL$ ($r^2 = 0.996$; $n = 64$).

RESULTS

Egg distribution

The great majority of eggs of *Notothernia coriiceps* was recorded by RMT hauls fishing between 300 m and the surface. They occurred in neritic and oceanic waters far offshore over water depths ranging from 230 to 2600 m. On two occasions, one neuston tow in spring 1977 and another tow in spring 1988 were eggs found at the sea surface.

During the spawning season in May-June (1986), eggs were abundant and widespread, and were found far to the south of the Palmer Archipelago (Kellermann and Schadwinkel, 1991). In spring (October-December), eggs containing embryos at an advanced developmental stage were found during all cruises to the Antarctic Peninsula. In spring 1977, 1983 and 1984 they occurred in shelf and oceanic waters of the Bransfield Strait and its eastern approaches, in the Antarctic Sound and in the north-western Weddell Sea (Fig. 1a-c). Eggs were frequently obtained around Elephant Island. The northernmost record was made at 60°00'S. In spring 1987, sampling was extended to the south-west as far as Adelaide Island, but eggs were confined to Bransfield Strait and adjacent waters

(Fig. 1d). Mostly single eggs occurred in the RMT with maxima of 2-6 per tow (Table I).

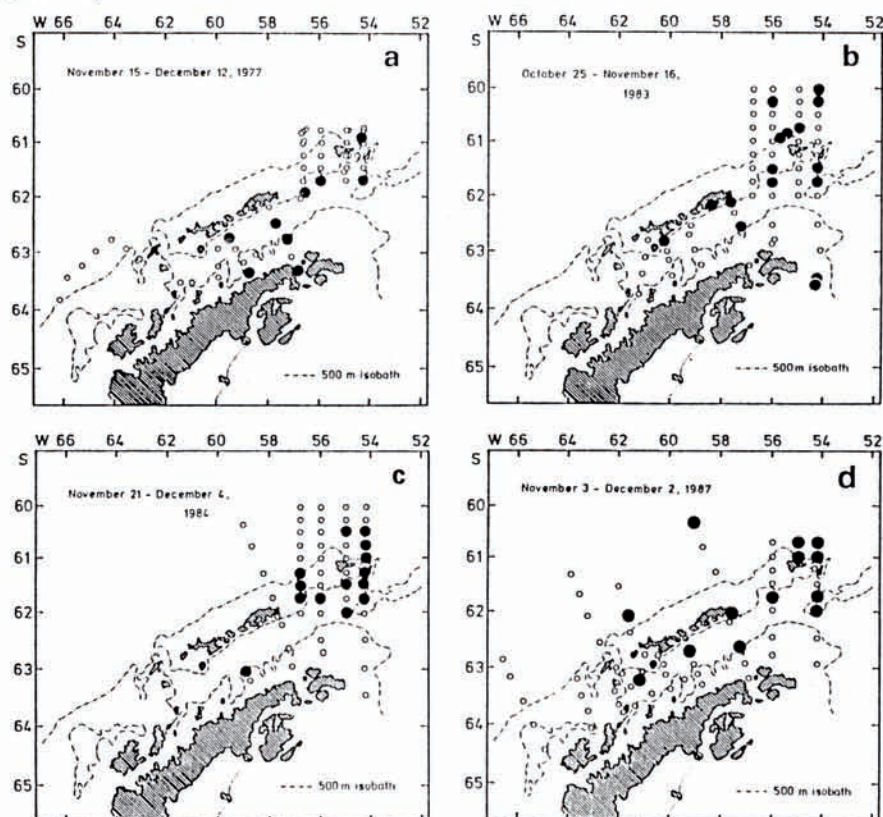


Fig. 1. - Distribution of eggs of *Notothenia coriiceps* (dots) in austral spring of the years 1977 (a), 1983 (b), 1984 (c) and 1987 (d) in Bransfield Strait and adjacent waters. All eggs contained embryos at an advanced developmental stage.

Table I. - *Notothenia coriiceps*. Egg sizes in mm (mean diameter $\pm$ sd, range, 95% confidence limits), no. of eggs (n), frequency (no. of tows containing eggs as percentage of total no. of tows), and no. of eggs per tow collected during the spring of 1977, 1983, 1984, 1986, and 1987. In 1986, only stations to the east of the Palmer Archipelago were considered to allow for comparison between years (data from Kellermann and Schadwinkel, 1991).

	YEARS				
	1977	1983	1984	1986	1987
Mean diameter	4.40 $\pm$ 0.23	4.30 $\pm$ 0.16	4.39 $\pm$ 0.17	4.53 $\pm$ 0.25	4.23 $\pm$ 0.19
95% Conf. Interv.	4.27-4.53	4.24-4.36	4.33-4.45	4.49-4.57	4.14-4.32
Range	3.8-4.7	4.0-4.6	4.1-4.7	3.9-5.0	3.9-4.6
Number of eggs	12	25	34	137	18
Frequency	16.1	26.2	26.9	40.7	23.6
Eggs per tow	1-2	1-3	1-6	1-44	1-6

In spring 1983, a few stratified tows were made to the north of Elephant Island. One of these yielded eggs at 275-225 m and at 25.0 m. In spring 1988 eggs were mostly collected by RMT hauls ($n = 16$ in 8 tows), and only once by a neuston haul ($n = 5$). Eggs were found along the ice edge in open waters as well as under ice cover. In the vertically stratified RMT hauls, eggs occurred in all depth strata between 300m and the surface.

In November-December 1975, 10 eggs were collected at four of the southernmost stations ($59^{\circ}10'S - 60^{\circ}00'S$) of the transects across the Scotia Sea between 42° and 52° W (cf. Fig. 3).

Egg size

Egg diameters in spring varied little between years (Table I). 95 % confidence intervals overlapped largely, and a Kolmogoroff-Smirnoff test (K-S at $p < 0.05$) did not indicate differences between egg size frequencies in the respective years. However, diameters of recently spawned eggs collected in early winter 1986 (Kellermann and Schadwinkel, 1991) were significantly larger than those caught in spring of the other years (t-test, K-S test at $p < 0.05$) (Fig. 2).

Larval distribution

During the 1975/76 expedition, larvae of *Notothenia coriiceps* were found dispersed across the Scotia Sea and off South Georgia (Fig. 3). In late November and during the first half of December they were found in the southern and in the central Scotia Sea on the SW-NE transect towards South Georgia. The southernmost record was made at 60° S. In late February, three transforming larvae were caught in the southern Scotia Sea. In late March and the first half of April, transforming larvae and juveniles were found in the central Scotia Sea and off South Georgia as far as 26° W (Fig. 3). The stations worked in Bransfield Strait in January/February did not yield any larval or juvenile *N. coriiceps* despite intensive sampling with neuston and RMT nets.

In November-December, the majority of larvae ($n = 42$) were caught by the neuston-net, mostly by the upper net fishing at the surface, and only a few ($n = 8$) by RMT hauls fishing through the surface. Up to 16 larvae were found in one neuston tow. The specimens in March-April ($n = 15$) were all caught by the upper neuston-net, except one found in a pelagic krill trawl. Up to seven fish occurred in one tow.

The 1977/78 expedition caught larval *N. coriiceps* only in February, in the eastern Scotia Sea and off South Georgia (Fig. 4). A single juvenile was found off the South Orkney Islands (Fig. 4). The fish occurred in the lower neuston-net ($n = 4$), and in the RMT ($n = 3$). The cruise legs worked in the Bransfield Strait and adjacent waters failed to record *N. coriiceps* despite intensive sampling with neuston and RMT nets.

During the later expeditions in spring of 1983-1988 to the Antarctic Peninsula, only few larvae were obtained. In late November 1984, a single juvenile (60 mm SL), and two larvae (14.0 mm SL) were caught in Elephant Island waters along with eggs at an advanced developmental stage. Two transforming larvae (33.8, 35.0 mm SL) were collected in the southern Drake Passage in mid March 1985. Two 'blue phase' juveniles of 55 and 57 mm SL were caught in a beam trawl to the south of Elephant Island in mid December 1987 (Kock, pers. comm.). No larvae were recorded in Antarctic Peninsula waters in summer, fall or early winter (Kellermann, 1989a).

Larval sizes, hatch and growth

The standard lengths of larval and juvenile *Notothenia coriiceps* captured during the 1975/76 season are given in table II. The data were broken down by the time periods during which they were collected to detect growth in length.

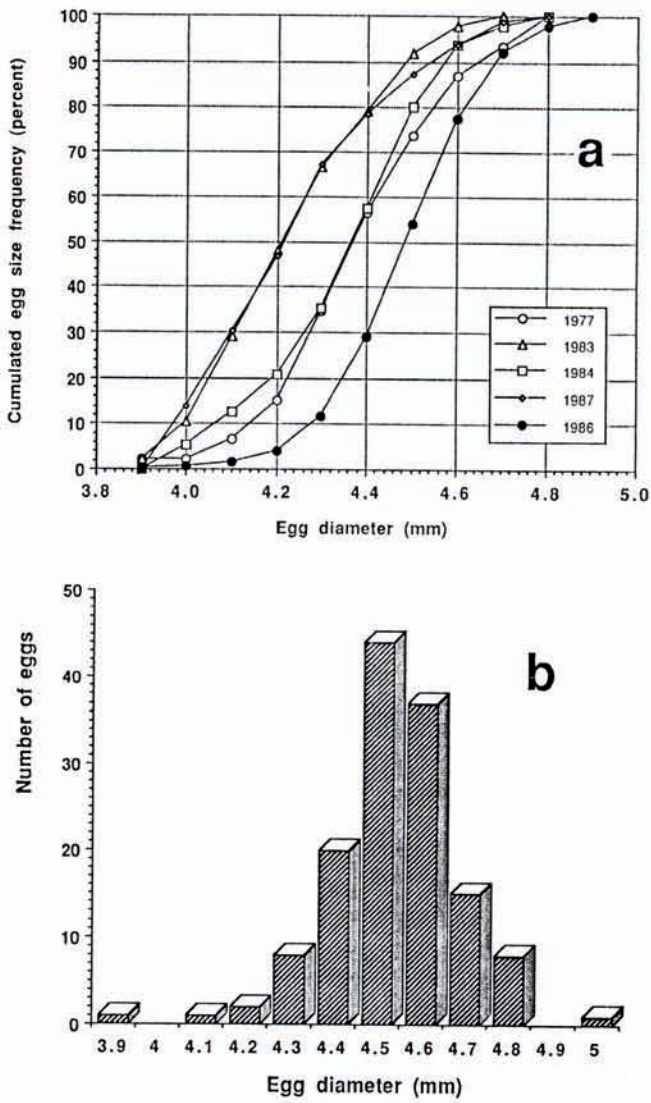


Fig. 2. - Size frequency of *Notothenia coriiceps* eggs in spring of the years 1977, 1983, 1984, 1987 and in winter 1986 (a, smoothed data), and only in winter 1986 (b). For the number of eggs measured cf. table I. Data from 1986 from Kellermann and Schadwinkel (1991).

Latitudinal variations may be partly involved in the observed differences between time periods, but some of the stations worked in early and late December were in the same area. Confidence limits of mean lengths did not overlap, indicating significant differences assumed to reflect larval growth. When the length data were plotted versus days (starting November 1), a logarithmic function gave the best fit to the data (Fig. 5). The length data from the remaining years were similar at comparable time periods. Hatching may be estimated to occur in late November through mid December.

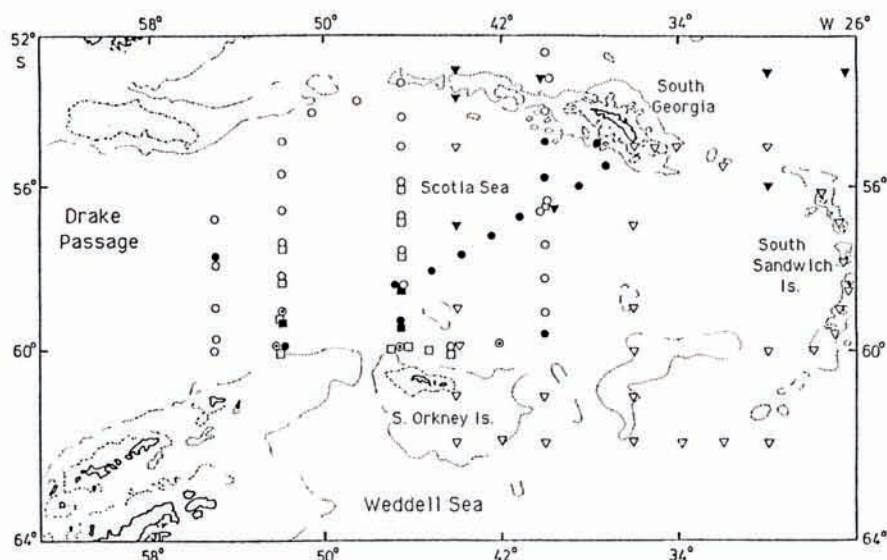


Fig. 3. - Distribution of larval and juvenile *Notothenia coriiceps* during the austral summer season 1975-76. Circles: stations worked 28 November - 27 December 1975. Squares: stations worked 24-30 February 1976. Arrowheads: stations worked 23 March - 4 April 1976. Filled symbols indicate positive catches, open symbols no records. Station grids worked at the Antarctic Peninsula and at South Georgia not shown (see Sahrhage *et al.*, 1978).

Table II. - *Notothenia coriiceps*. Larval and juvenile standard lengths in mm (mean $\pm$ sd, 95% confidence limits, range) and no. (n) of larvae and juveniles caught in spring, summer and fall of the 1975/76 season. Neuston and RMT 1+8 nets.

Time period	Mean $\pm$ sd	95% cl	Range	n
November 28 - December 6	14.0 $\pm$ 1.1	13.5-14.5	12.2-16.8	22
December 22 - 27	17.6 $\pm$ 1.4	17.0-18.2	14.6-20.2	20
February 24 - 29	-	-	22.5-29.3	3
March 23 - April 17	35.5 $\pm$ 4.7	33.1-37.8	29.5-47.0	15

DISCUSSION

The vertical distribution of eggs in the field during spawning in early winter suggested that they become buoyant after fertilization and ascend to the surface (Kellermann and Schadwinkel, 1991). The deep records made in spring (1984 and 1988) show that eggs may occur throughout the top 300 meters of the water column shortly before hatching. The field data further suggest that eggs are pelagic during the entire incubation period. Previous experimental work using artificially fertilized eggs of *Notothenia coriiceps* had produced contradictory results (White *et al.*, 1982); eggs reared at South Georgia remained floating during the entire incubation period, while at the South Orkney Islands they sank to the bottom of

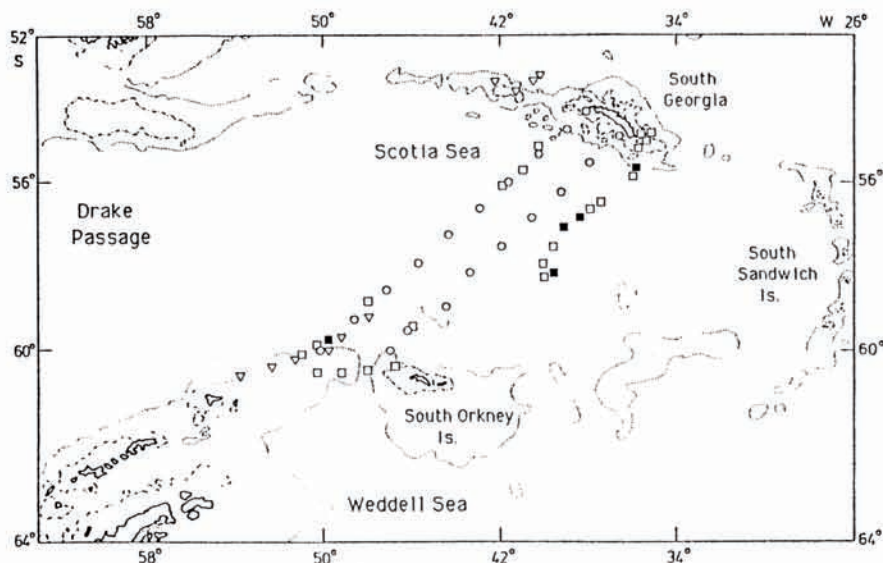


Fig. 4. - Distribution of larval and juvenile *Notothenia coriiceps* during the austral summer season 1977-78. Circles: stations worked 12-16 November (lower SW-NE transect), and 7-14 December 1977 (upper SW-NE transect), respectively. Squares: stations worked 21-28 January, and 31 January - 1 February 1978. Arrowheads: stations worked 5-7 March and 28-29 March 1978. Filled symbols indicate positive catches, open symbols no records. Station grids worked at the Antarctic Peninsula and at South Georgia not shown (see Hempel *et al.*, 1979).

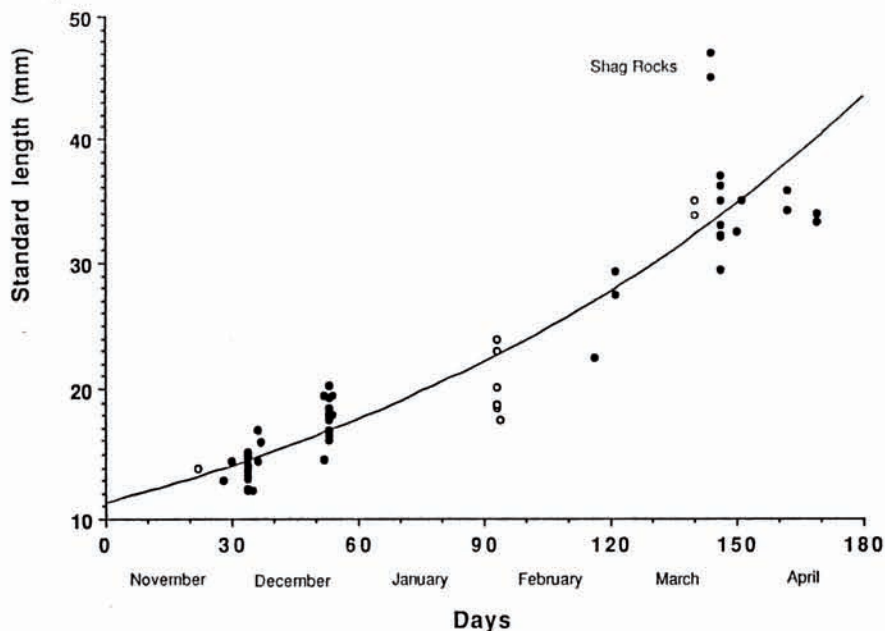


Fig. 5. - Standard lengths of larval and juvenile *Notothenia coriiceps* caught during the 1975-76 austral summer season (dots), and during the remaining years of this study (circles). The regression curve was fitted to mean lengths in spring, summer and fall 1975-76 (see Table 2), and fits the equation $SL = 11.2 * 10 (3.26e-3 \text{ days})$, $r^2 = 0.921$ ($n = 3$, $p < 0.05$). Fresh length at hatch is 12.2-16.3 mm (Kellermann, 1990).

the tanks during the experiment, which was due to increased salinity because of evaporation from the culture vessels (White, pers. comm.).

The vertical distribution of pelagic eggs is determined by their specific density which may increase with age, as observed for e.g., Atlantic halibut eggs, and by the physical stratification of the water column (Haug *et al.*, 1986). During the spawning season in early winter, a strong density gradient in the upper 500 m of the water column can be expected due to sea-ice formation and subsequent deep convective mixing (Stein, 1986, 1989). This would facilitate the ascent of the eggs to the surface. Egg size and surface structure may have a significant influence on their vertical transport, with the former being directly related to ascent rates, while a sculptured chorionic surface has the reverse effect (Robertson, 1981). Eggs of *N. coriiceps* are relatively large and have a smooth and poorly structured chorionic surface (Riehl and Kock, 1989), pointing to a rapid ascent to the sea surface under appropriate hydrographical conditions. Since the larvae of *N. coriiceps* are found in the neuston, eggs at the final stage of development probably occur close to the sea surface before hatching. However, if age-specific changes occur in *N. coriiceps* eggs similar to other species (see Haug *et al.*, 1986), the eggs would sink before hatching as surface waters in spring may become less dense by the influence of melting sea-ice. Experimental work is needed to study the density changes of the pelagic eggs of *N. coriiceps* during the entire incubation period.

The distribution of eggs in winter and spring in Bransfield Strait and adjacent waters suggests that eggs are drifted out of the Strait into oceanic waters. The currents in spring flow to the east and north-east (Clowes, 1934, Stein, 1986), and disperse the eggs into the Antarctic Circumpolar Current in the northern Weddell Sea and southern Scotia Sea. This egg drift is confirmed by the occurrence of larvae which were confined to oceanic waters to the north of 61° S. The distribution of larvae, especially in the 1975-76 season suggests a larval drift to the north-east across the Scotia Sea. Except for the Weddell-Scotia-Confluence where meanders and eddies may occur (Anon., 1983), the general flow direction in the Scotia Sea is to the north-east (Clowes, 1933; Sievers and Nowlin, 1989). This was also the case during the 1975-76 season as indicated by the geostrophic flow at the sea surface (Stein, 1989). Current velocities may be in the order of 12-25 cm/s (Stein, 1989), which, given the lower value, seem strong enough for a neustonic larva to be passively driven as far as South Georgia during one summer. Thus, gene flow by advection to other populations seems likely.

Hatching commences in late November off the Antarctic Peninsula. The complete lack of larvae in Bransfield Strait and adjacent waters in summer and fall despite intensive sampling by both RMT and neuston-net (in 1975-76 and 1977-78) suggests that most of the larvae are exported by the drift, if not the entire population. Early stages of *N. coriiceps* were also lacking during other ichthyoplankton summer surveys (e.g., Asencio and Mujica, 1986; Sinque *et al.*, 1986, White and North, 1987). The wide off-shore dispersal of fingerling stages observed at South Georgia (White *et al.*, 1982) is confirmed by the present results. In the Antarctic Peninsula area, recruitment is likely to occur by transport of pelagic juveniles with the Antarctic Circumpolar Current from the south-west. This may be indicated by the few records off the South Shetland Islands in this study, and by incidental catches of juveniles in pelagic krill trawls in summer (Rembiszewski *et al.*, 1978). A wide oceanic drift, as implied by the postulated large scale circumantarctic recruitment with the Circumpolar Current as its vehicle, is not uncommon in teleost fishes. In the Armorhead *Pseudopentaceros wheeleri*, the pelagic larvae and juvenile fishes are widely dispersed from spawning grounds at Pacific seamounts and may travel for two years in a northeast Pacific gyral system before they recruit to the seamount populations (Boehlert and Sasaki, 1988). A similar, circumantarctic drift and recruitment pattern may exist not only in *N. coriiceps*, but also in other nototheniid species with pelagic eggs and a wide circumantarctic distribution, e.g., in *Dissostichus eleginoides*.

White *et al.* (1982) found that laboratory growth rates of *N. coriiceps* larvae were sufficient to reach the size of transformation to the demersal stage within the first summer. Their growth curve is very similar to that found by measurements of larvae caught in the field during this study. Nearshore records of larvae at South Georgia were made from late December onward (White *et al.*, 1982). However, 'blue phase' juveniles of 70-80 mm SL have been reported (Johnston and Camm, 1987), and the pelagic juveniles of 55-60 mm SL caught in spring and summer are unlikely to belong to age group 0. Thus, juvenile fishes may spend the winter and second summer in the midwaters. Such fishes may have failed to find suitable shelf areas, and become recruits to the demersal juvenile population after delayed transformation.

The spawning migration of adult *N. coriiceps* into deeper water probably accounts for the wide dispersal of the pelagic eggs. A spawning migration into deeper, slope waters was reported for *D. eleginoides* (Duhamel, 1987), and the pelagic eggs were found far offshore before hatching (Kellermann, 1990). During the last glacial maximum, Antarctic shelf areas were largely covered by ice-shelves (Grobe, 1988) which must have resulted in significant disturbances of the shallow water fauna (Andriashev, 1987). The spawning migration of the shallow water fish *N. coriiceps* may be a reminiscence of that period when spawning grounds were limited and confined to greater depths. Primary production peaks were likely to occur during shorter periods than today due to the greater extent of sea ice and may have been spatially highly variable. The buoyant eggs provide a vehicle for a rapid ascent to the euphotic zone, and for a wide dispersal of larvae to increase encounters with high food abundance. Therefore, pelagic eggs in Antarctic notothenioid fishes may well be an adaptation that evolved under environmental conditions prevailing during the last glacial maximum, and have ultimately contributed to the extensive, circumantarctic distribution. A passive drift during the egg stage conserves energy since no swimming activity of larvae is involved. On the other hand, the extended pelagic development increases the risk of predation. However, the large and smooth eggs are probably more difficult to handle and ingest for most planktonic predators than the free swimming larvae. Thus, the low relative fecundity of *N. coriiceps*, that is, the low number of offspring per unit body mass may be balanced by reduced predation in the midwaters due to the large egg size.

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